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ABSTRACT

The holotype of the species, *Domninoides mimicus*, is based on one tooth. Described in the present report is material containing a practically complete dentition and many postcranial elements which definitely belong with the teeth. This species is closely related to *Domninoides valentinensis* described by Reed (1962), but some of the antemolars in *valentinensis* are misidentified. The tooth formula for *valentinensis* should be $\frac{3}{3}$? $\frac{?}{1}$ $\frac{?}{3}$ $\frac{?}{3}$ and for *mimicus* is $\frac{2}{2}$ $\frac{1}{2}$ $\frac{?}{3}$ $\frac{3}{3}$. Development of the cingula on the upper and lower molars in *mimicus* is conspicuous. Because of similar features in the postcranial bones, the Clarendonian mole may be as fossorial as *Scalopus*, probably the most fossorial extant North American mole.

INTRODUCTION

The Burge Clarendonian Fauna of north-central Nebraska is known principally by several species of large plains-dwelling ungulates, remains of which supposedly were deposited in stream channels under flood conditions. Few remains of small mammals, namely rodents and insectivores, were preserved because of this rapid water transport (Webb, 1969). The fossil talpid described below, which was found in the Burge Member of the Valentine Formation by Larry Langer and generously presented to the Frick Collection at the American Museum of Natural History, is a superb specimen not only in quality of preservation but also because postcranial elements are definitely associated with the skull.

The mole is large and belongs to the genus *Domninoides*. Wilson (1968) first described the species as *Domninoides mimicus*. The type material consists of isolated teeth and associated bone fragments from the WaKeeney local fauna of the Ogallala Formation in Trego County, Kansas. Wilson believed this fauna to be younger than that from the Valentine in Nebraska (from Norden Bridge to Burge) and assigned it to the middle or late Clarendonian.

Domninoides mimicus is closely related to *Domninoides valentinensis* Reed, 1962, from the older Crookston Bridge Member of the Valentine Formation, sediments thought to be Barstovian. It is also similar to *Domninoides riparensis* Green, 1956, a slightly smaller mole from the Ogallala-Wolf Creek Fauna of South Dakota, where the age is undifferentiated but thought to be late Clarendonian by Green.

Species of the genus *Domninoides* have, on

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the whole, few differences in the dilamdodont pattern of the upper molars, and all have wide anterior cingula on the lower second and third molars. Differences among the species in the genus occur primarily (1) in the general size (as with the small *D. platybrachys*), and (2) in the number of antemolars present in the lower jaw.

MATERIALS AND METHODS

I have followed Hutchison's (1968) classification of talpids as well as his use of names for cusps and osteological features.

Measurements were taken with Anderson's (1968) craniometer attached to a Wild M5 stereomicroscope. Each tooth was measured individually so as better to compare it with isolated teeth that may be found. Measurements are to tenths of millimeters. For measurement of the lower teeth in the mandible, the superior lingual edge of the dentary should be parallel with the surface of the stage. The mandible was turned slightly to make the superior surface of each tooth parallel to the surface of the stage, and the crosshair was aligned parallel to the lingual surface of the tooth. Both trigonid and talonid widths are recorded. Length is taken with the crosshair aligned perpendicularly to the width axis. With the superior surface of the upper molars parallel to the surface of the stage, each molar is more easily measured by using the bases of the paracone and metacone as orienting points. Using these points, greatest length can be recorded and greatest width in a line perpendicular to the length axis. Greatest length of P^4 is taken in a line as parallel as possible to the labial surface and width perpendicular to it. The scale in each of the drawings is equal to one millimeter.

Fossil talpid material examined for comparisons include *Domninoides mimicus* type material from the University of Michigan, described by Wilson (1968) and *Domninoides valentinensis* type material from the University of California, described by Reed (1962). Readers are referred to those publications for lists of teeth and bones included in each.

The following abbreviations are used:

AMNH, Recent mammal collections, Department of Mammalogy, the American Museum of Natural History, New York

F:AM, Frick Collection, the American Museum of Natural History, New York

UC, University of California Museum of Paleontology, Berkeley

UM, University of Michigan Museum of Paleontology, Ann Arbor

MSB, University of New Mexico Museum of Southwestern Biology, Albuquerque

Recent talpids used for comparison are as follows:

AMNH 206 *Desmana moschata*, skull and partial skeleton

AMNH 140405 *Parascalops breweri*, skull and skeleton

AMNH 35234 *Parascalops breweri*, skeleton only

MSB 13187 *Parascalops breweri*, skull only

AMNH 145481 *Scapanus latimanus latimanus*, skull and skeleton

AMNH 121212 *Scapanus orarius orarius*, skull and skeleton

AMNH 38248 *Scapanus townsendii*, skull only

MSB 25243 *Scapanus townsendii*, skull only

AMNH 70520 *Scalopus aquaticus aquaticus*, skull and skeleton

AMNH 145480 *Scalopus a. machrinoides*, skull and skeleton

MSB 11416 *Scalopus a. machrinoides*, skull and skeleton

MSB 13186 *Scalopus a. machrinoides*, skull only

AMNH 123819 *Scalopus a. machrinus*, skull and skeleton

AMNH 63789 *Scalopus a. machrinus*, skull and skeleton

MSB 9154 *Scalopus a. machrinus*, skull only

AMNH 99695 *Talpa europaea*, skull and skeleton

SYSTEMATICS
ORDER INSECTIVORA

FAMILY TALPIDAE FISCHER VON WALDHEIM, 1817

SUBFAMILY TALPINAE FISCHER VON WALDHEIM, 1817

TRIBE SCALOPINI DOBSON, 1883

Domninoides mimicus Wilson, 1968

MATERIAL: F:AM 74966; partial skull, palate with both tooth rows present, right tooth

row with P^4, M^{1-3} and roots only of C^1, P^{1-3}; left tooth row with P^{3-4}, M^{1-2}, alveolus of I^2 or I^3, fragment of C^1 above alveolus, roots of P^{1-2}; both mandibles with ascending rami, dentary condyles, and angular processes present, right mandible with P_4, M_{1-3}, partial alveolus of I_1, I_2, and fragments of P_{2-3} above alveolus; left mandible with P_4, M_{1-3}, fragments of I_1 and C_1 above alveolus, P_{2-3} only partial roots. The teeth are moderately worn. Postcranial elements include proximal end of left scapula, left ulna, left radius, and left femur.

HORIZON AND LOCALITY: Late Miocene, Clarendonian, near top of Burge Member of Valentine Formation, from head of small draw on east side of canyon at head of Cramer Creek, Norden 1950 Quad., in center of SE ¼ of SE ¼ Sect. 30, T. 34 N., R. 24 W., Keyapaha Co., Nebraska.

DIAGNOSIS: The specimen is a large fossorial mole about the size of Recent *Scalopus* and *Scapanus*, a dental formula of $\frac{2}{2} \frac{1}{1} \frac{4}{3} \frac{3}{3}$ and a short rostrum. Although the lower molars (M_{2-3}) are similar to *Domninoides valentinensis* Reed, 1962, in morphology and size, the anterior dentition of *mimicus* differs in having a conical P_4 with no anterior cusp, three lower premolars (as has *valentinensis*, but Reed described four) with P_{2-3} single rooted (although P_2 has a fused double root; x-ray, fig. 1), no canine, and a large I_2 (as has *D. valentinensis*, but not described by Reed). M_1 has an anterior cuspule, slight anterior cingulum, and less than prominent metastylid. M^{1-2} are large, squarish teeth with anterior and posterior cingula extending from the protocone and smaller metaconule, respectively, to the labial side. M^3 is triangular with an anterior cingulum only, and P^4 is similar to the chipped one of *D. valentinensis* with bladelike paracone and lingual cusp. The postcranial elements, scapula, ulna, radius, and femur, are large and robust, and their size and configuration are typical of the same bones in the more fossorial Recent talpids (*Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*). The scapula has both an infraspinatus fossa extending the length of the shaft and a foramen for the suprascapular nerve piercing the acromion process. Both scapular features occurring to-

gether make the fossil similar to those in *Parascalops* and *Scalopoides* (fossa deeper here) and taken individually distinguish it as a member of the tribe Scalopini and not a member of the Talpini (lacks fossa) or the Urotrichini (lacks foramen). The ulna has a semilunar notch more than a semicircle in shape, making it slightly more developed than that in *Domninoides valentinensis*, much more developed than that in *Scalopoides*, but similar to the notch of Recent *Scalopus*. Also, the ulna of the Scalopini can be distinguished from that of the Talpini because of its long, cylindrical styloid process and less overhang of the radial articular facet on the abductor fossa. The radius bears a flattened capitular process like that in *Parascalops* but unlike the oblique one in *Scalopoides* and the rounded one in *Scapanus* and *Scalopus*. The femur is rugged with trochanters well-developed as in Recent fossorial moles.

DESCRIPTION OF SKULL AND TEETH

SKULL: The fragmented skull, primarily a rostrum with upper teeth (fig. 2), has a partially distinguishable infraorbital foramen on the left side of the dorsal surface. Compared to Recent moles, the rostrum is short with a flexure at P^2. Posterior to the widest part of the rostrum, roots of the zygomatic arches emerge (approximately at the mesostyles of M^2). On the ventral side of the skull, the palate is partially intact; the posterior part of the palate is missing. The incisive foramina are just distinguishable medial and anterior to the canines.

Of the upper antemolars, no incisors are present, although an alveolus is present for the left I^2 or I^3 and possibly a partial one for an enlarged I^1. The canine and premolars $^{1-3}$ are all single rooted but the root of the canine is larger. Small and complete, the left P^3 is a conical paracone with a slight posterior shelf. The large fourth premolar is a triangular, molariform tooth with a high conical paracone (as high as the metacone of M^1) and posterior bladelike ridge that extends to the posterior labial portion of the tooth. An anterior accessory cusp starts the slight cingulum that extends to the lingual face where the protocone emerges
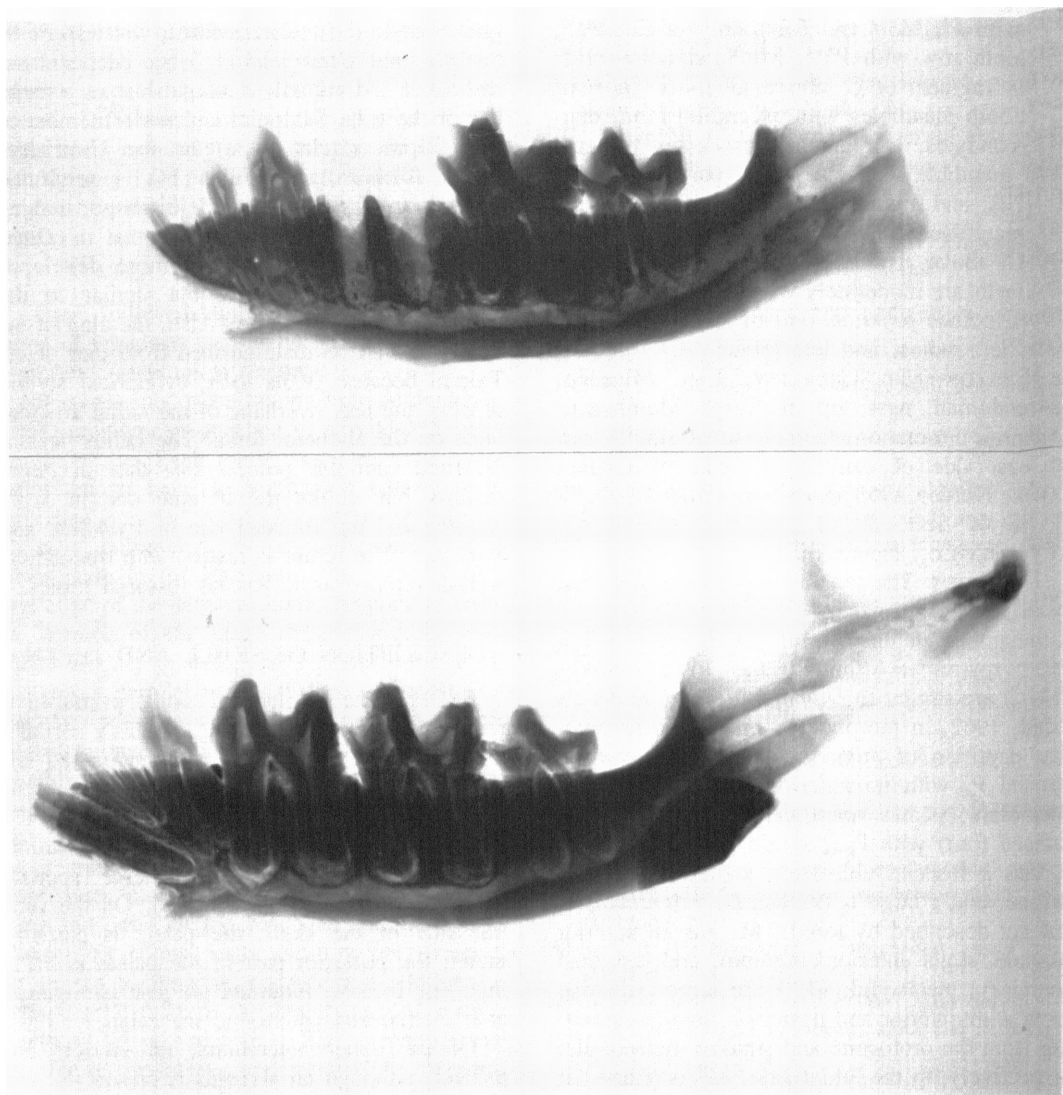
FIG. 1. X-ray of side views of left dentary of *Domninoides valentinensis* (UCMP 33152, top) and right dentary of *Domninoides mimicus* (F:AM 74966, bottom).

posterior to the paracone. From the protocone, the cingulum dips and extends across the posterior face and ends labially as a posterior accessory cuspule at the base of the bladelike posterior ridge of the paracone. The groove between the two major cusps is narrow anterolingually and wide and deep posteriorly. The tooth appears to have three roots, two labial and one lingual.

The first upper molar is a squarish tooth bordered on three sides by cingula or lingual cusps. Starting with a small anterior accessory cuspule, the cingulum extends across the anterior face around to the lingual side where the protocone and metaconule (Reed's hypocone, 1962) arise. From the metaconule the posterior cingulum runs labially to join the metastyle. Lacking a parastyle, the paracone is a bladelike

cusp, second to the metacone in height. This feature identifies "M^1 or M^2" (UM V55737) of Wilson's (1968) type material of *D. mimicus* as an M^1. Mesostyles are twinned and the protofossa, although deep, is not so deep as the wide anterior and posterior cingula. Between mesostyles and the metastyle is a small labial cusp that nearly encloses a pitlike stylar shelf. This cusp is not present on M^1 of the holotype. A paraconule is present, anterior to the protocone on the unworn M^1 of the holotype.

Although like the first upper molar, the second has a distinct parastyle and the anterior and posterior cingula do not extend so far labially. Both anterior and posterior stylar shelves on both left and right second molars are pitlike and partially closed off by small labial cusps. Unfortunately, there is no M^2 of the type material with which to compare to see if these small cusps are present. On the lingual side the area between the protocone and metaconule is worn and the cusps are not distinguishable.

The third molar, smallest of the upper molars, is triangular. The anterior cingulum extends from beneath the parastyle to the protocone, which is posterior to the paracone, and the metaconule, which is separate from the protocone, lies next to the metacone. The paracone is the same height as the metacone, which is bladelike and lacks a metastyle. A posterior cingulum is not present and the anterior stylar shelf is bordered by a low ridge.

MANDIBLE: The mandibles themselves are sturdy, deep and short, with ascending rami at 90 degree angles to the tooth-bearing portion (figs. 3 and 4). Two mental foramina lie beneath P$_4$, which is also the point where the symphysis appears to end on the lingual side.
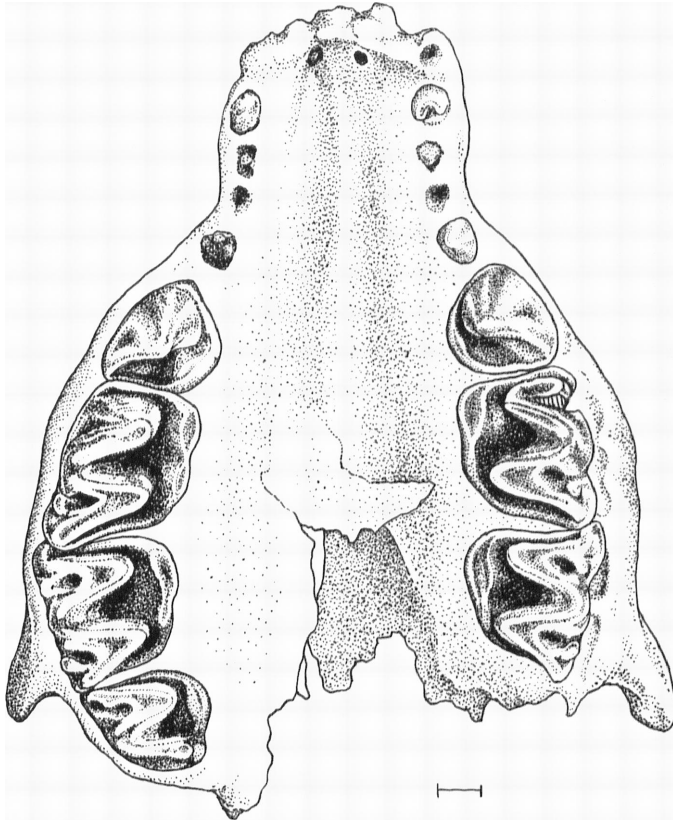

FIG. 2. Occlusal view of upper teeth and rostrum of *D. mimicus* (F:AM 74966).
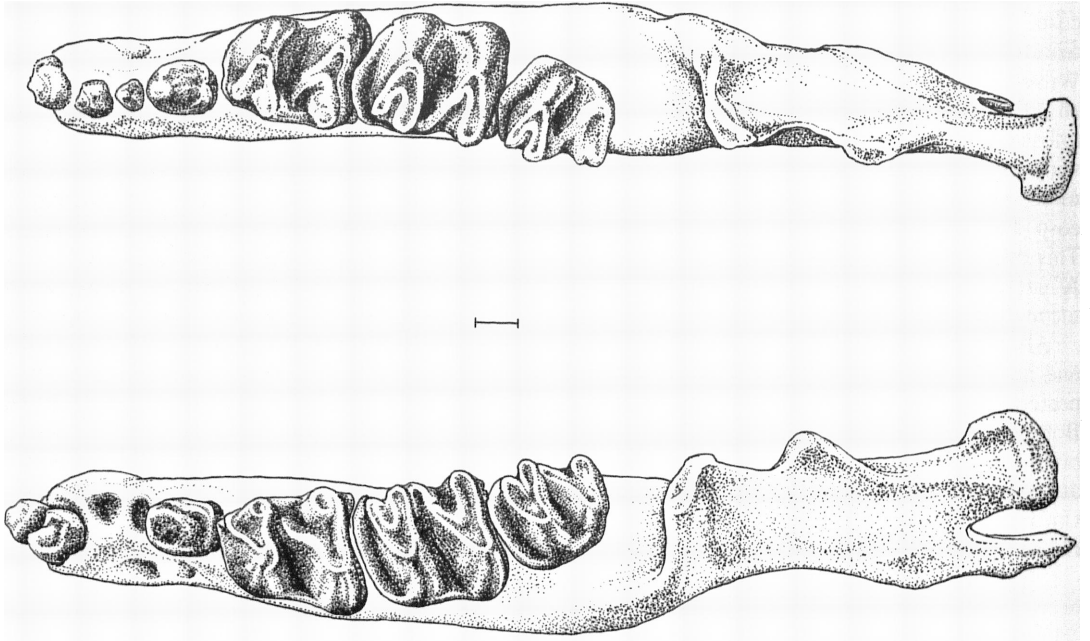
FIG. 3. Occlusal view of teeth of both dentaries of *D. mimicus* (F:AM 74966).

The angular process is wide and not so thin and delicate. The dentary condyle is transversely elongate with an additional articular surface on the lingual side, giving it an L-shaped outline.

Of the lower antemolars, the most anterior incisor present is the fragmented left I_1 (fig. 4), an obliquely ovate tooth in the same plane as the mandibular symphysis. This tooth is followed by a hypertrophied I_2. Both the large I_2 and the small I_1 are in a procumbent position and are close together. The single-rooted I_2 is also larger than the first two premolars (P_{2-3}). The three remaining antemolars, P_{2-4}, are closely spaced with P_3 smaller than P_2, and both P_2 and P_3 smaller than P_4. P_2 is transversely ovoid with a fused double root and bears a slight posterior heel and the smaller, single-rooted P_3 is similar in shape but more peglike. Both are chipped. Conical and double rooted, P_4 bears a posterior shelf and cingulum that starts on the lingual side, slightly posterior to the paracone, and terminates in a small cusp (protoconid?) at the posterior lingual corner.

The first lower molar is noticeably different from the second and third lower molars in bear-ing a short narrow cingulum with small anterior cuspule, low paraconid, and a trigonid that is smaller than the talonid. Of the labial cusps, the protoconid is highest, followed by the hypoconid. The cristid obliqua extends ante-rolingually from the hypoconid to a metastylar ridge that extends posteriorly from the meta-conid. This ridge blocks most of the entrance to the postfossid (talonid basin) and makes a triangular basin with the base of the entoconid. The hypoflexid is moderately deep and is la-bially bordered by a small cingulum. A small posterior cingulum is apparent in two parts, one from the labial side that does not extend across the posterior face and another that lies behind the entoconid as a triangular, posterior acces-sory cuspid. In the type material of *D. mimicus* the isolated unworn M_1 has the slight posterior cingulum extending across the entire posterior face. Both the slight anterior and posterior cingula seem to become less apparent and even obliterated with wear.

A larger tooth than the first, the second lower molar bears a wide anterior cingulum which starts on the lingual side beneath the

paraconid and extends as a shelflike ridge across most of the anterior face of the molar. Because the ridgelike cristid obliqua attaches to a more distinct metastylid, the postfossid remains open lingually. The paraconid is nearly the same height as the metaconid and the trigonid and talonid are nearly equal (table 1). Possibly because of specific variation, M_2 on which the holotype is based has a smaller talonid relative to the trigonid and gives the tooth a less rectangular appearance. The hypoflexid with labial cingulum is deeper than that of the first molar and the slight posterior cingulum appears to be in two parts as in M_1. M_2 of the holotype bears only the small triangular accessory cuspid posterior to the entoconid.

The third lower molar also bears a wide anterior cingulum, which completely extends across the anterior face of the tooth. The cingulum of M_3s of the type material appear especially wide and deep toward the labial side. Although not so prominent as in M_2 (actually more like M_1), the metastylid exists and the postfossid is present only as a notch anterior to the low, wide entoconid. There is no posterior cingulum, but there is a small labial cingulum that borders the deep hypoflexid.

COMPARISONS OF TEETH

Domninoides mimicus resembles *Domninoides valentinensis* described by Reed in 1962. Major differences between the two arise in the anterior dentition of the lower teeth.

Hutchison (1968), having seen most known Miocene and Pliocene records of the genus, suspects that differences in this region might be useful in delineating species of *Domninoides*. An explanation of tooth loss and hypertrophy pattern is taken from Zeigler (1971) and will follow in the discussion section.

After seeing the type of *D. valentinensis* and examining an x-ray of it (fig. 1), I amend Reed's description slightly. The partial alveoli for the incisors, not described before, are possibly positions for a hypertrophied I_2 and a very small labial I_3 (no teeth are present). The first tooth present described as P_1 is, I believe, a small, conical single-rooted canine, and P_1 has already been lost evolutionarily (Zeigler, 1971). Although at first doubtful, I am now willing to accept the fact that P_2 has two roots. Hutchison has found this double-rooted condition to occur in recently found specimens of *D. valentinensis* (personal commun.). P_3 is a single-rooted, bladelike tooth, has a prominent heel, and is as large or larger than P_2.

Using this amended description of *D. valentinensis*, the differences between it and *D. mimicus* can be more easily explained. The dentary of *D. mimicus* (AMNH) which is intact, bears three premolars, and I_2 and I_1 fragments in the left mandible. Because of the hypertrophy pattern of I_2 in Recent talpids (Zeigler, 1971), I believe that the second most anterior tooth is an enlarged I_2 and corresponds with the large alveolus for an incisor in *D. valentinensis*.
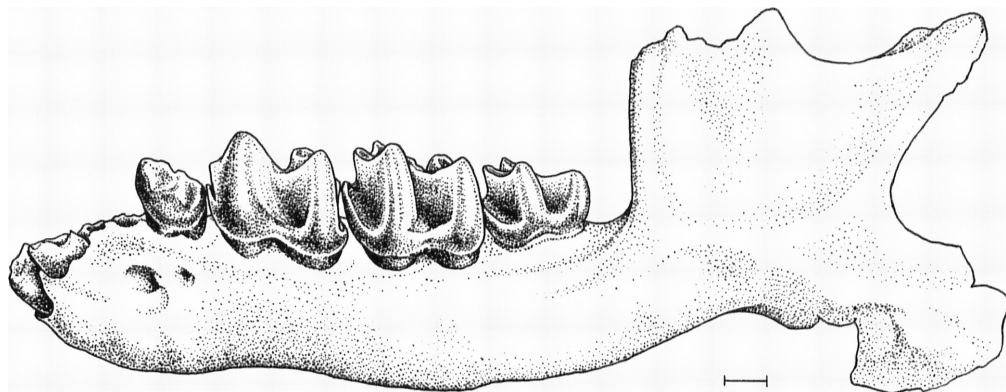

FIG. 4. Labial view of left dentary of *D. mimicus* (F:AM 74966).

TABLE 1

Measurements of teeth of *Domninoides mimicus*, F:AM 74966, in Millimeters[a]

Upper teeth		Length	Width	Lower teeth		Length	Width
P⁴	left	2.4	2.4	P₄	left	1.6	1.2
	right	2.4	2.3		right	1.6	1.2
M¹	left	3.5	3.5	M₁	left	3.2	2.1 trigonid 2.6 talonid
	right	3.6	3.4		right	3.2	2.0 2.5
M²	left	3.4	3.1	M₂	left	3.5	2.5 2.5
	right	3.3	3.1		right	3.3	2.5 2.0
M³	left	—	—	M₃	left	2.6	1.6 2.0
	right	2.2	2.5		right	2.6	1.6
M¹⁻³	left	10.5		M₁₋₃	left	9.0	
	right	—			right	9.0	
P¹-M³ (alv.)	left	13.4		P₂-M₃ (alv.)	left	11.6	
	right	—			right	12.1	

[a]Measurements of the skull include: least depth of jaw at M_1, left 3.7 mm. and right 3.6; greatest depth of jaw at M_2, left 3.8 and right 3.6; and width of palate at anterior edge of M^2 is 12.4 mm.

A small canine is present in *D. valentinensis* (described by Reed, 1962, as P_1), whereas none is present in *D. mimicus* (F:AM 74966). Neither species has P_1, and second premolars probably agree in number of roots: *D. valentinensis* with two and *D. mimicus* with a fused double root. Size of P_2s in the two species may be similar. Differing in shape, the peglike chipped P_3 of *D. mimicus* is smaller than the bladelike P_3 of *D. valentinensis*, which also has a prominent heel. Both are single rooted. Although more similar in size to P_4 of *D. mimicus* than the other premolars, P_4 of *D. valentinensis* bears an anterior cusp (this appears bladelike, but I believe the tooth is chipped) with a small labial cingulum extending from it around the paraconid to the posterior side where it ends in a low posterolingual heel (worn cusp?). P_4 of

D. mimicus has neither the anterior cusp nor the labial cingulum but, instead, has a conical paraconid and a distinct posterior heel that bears a cingulum on the lingual side, terminating in a small posterior cusp.

Compared to *Domninoides riparensis* Green, 1956 (not seen) *D. mimicus* like *D. valentinensis* has "No diastema between P_3 and P_4; slightly larger and more robust than *Domninoides riparensis*; metastylid definite on M_2" (Reed, 1962). Additional comparisons with *D. mimicus* are: *D. riparensis* with P_3 single rooted (Green, 1956, wrote that P_3 is double rooted but Hutchison, personal commun., believes this is a single-rooted tooth) and well-developed with a distinct heel (similar to *D. valentinensis*), P_4 with anterior cusp and labial cingulum (similar to *D. valentinensis*), M_1

smaller with distinct metastylid, M_2 with indistinct metastylids, and M_{2-3} with anterior cingulum possibly less broad. *Domninoides riparensis* appears (from drawing) to have cingulum extending labially around the base of the protoconid to the anterior cingulum in M_{1-3} (true on M_3 only in *D. valentinensis*). In summary, the teeth of *D. valentinensis* and *D. riparensis* are much alike in morphology, but both differ from the teeth of *D. mimicus*.

Further comparisons could probably be made among the molars of the three fossil species, but not having seen the actual specimen of *D. riparensis* makes comparisons from the rather inadequate drawing of Green's impossible. Differences in metastylids on the lower molars could well be due to individual variation or wear or both according to Hutchison (personal commun.).

Another specimen of *Domninoides* (not seen) from Fish Lake Valley, Nevada described by Clark, Dawson and Wood (1964) as *D.* cf. *riparensis* is worth being compared. Although similar in size and in most general characteristics to *D. riparensis*, the specimen differs in the following features: M_1 with small but distinct anterior cingulum that connects the anterolingual cuspule, M_3 with anterior cingulum that is more reduced bucally than in the type, metastylid indistinct on M_1 and prominent on M_2. These differences from the type of *D. riparensis* correspond with features of the larger *Domninoides mimicus*. Clark, Dawson and Wood (1964) believed that the variation between their specimen and *D. riparensis* could be accounted for by individual variation and degree of wear. This may be true, but, until more specimens are found, I do not think it can be verified.

Domninoides platybrachys (see Hutchison, 1968, p. 4) is named from a humerus. Recently Hutchison has found teeth that he believes are associated with that species (see Hutchison, 1968, fig. 67). I have seen these teeth, which are similar to other species of *Domninoides*, but they are much smaller and need not be compared.

A geologically older as well as contemporary genus to *Domninoides* is the genus *Scalopoides*, which includes moles that are generally less robust and less fossorial. Hutchison (1968) and Wilson (1960) both summarize differences between these two genera and elaborate on the less specialized characters of *Scalopoides*. In short, the lower teeth differ from *Domninoides* by being smaller, having P_{2-3} double rooted, lacking a metastylid on M_1 and well-developed on M_2 (reduced in *Domninoides*), talonid valley closed on M_2 (open in *Domninoides*), and the molars smaller and more or less mesodont. Upper molars of *Scalopoides* have never been compared with those in *Domninoides* because there has never been adequate material of the latter. Upper molars of *Scalopoides ripafodiator* Hutchison, 1968 (fig. 48), differ from *Domninoides mimicus* in the following ways: M^1 elongated and less quadrate in shape with anterior accessory cusp more prominent; a short, shelflike anterior cingulum present on the face of the M^1; a prominent rib ventral to the protocone, which appears relatively higher to its paracone than the same feature in *Domninoides*; and a parastyle more vestigal than in *D. mimicus*. M^2 has anterior and posterior cingula missing except as styles, protocone and metaconule not so prominent and lingual to paracone and metacone, respectively, and mesostyles only weakly twinned. M^3 has anterior cingulum lacking, mesostyles not twinned, and protocone and metaconule not prominent.

MacDonald (1963) named another species of *Domninoides* from the Arikareean and considered it to be the earliest record of the genus. Hutchison (1968, 1972) referred it to *Proscalops* on the basis of tooth morphology and similar postcranial material described by Reed and Turnbull, 1965. There are, however, similarities in the teeth with the genus *Domninoides*, especially in the development of the cingula on the lower molars. Curiously, Reed (1962) believed that the development of the anterior cingula on *"Domninoides evelynae"* lower molars was too great for the species to be included in the Proscalopinae.

Another proscalopine mole that may be confused with *Domninoides* is *Mesoscalops* (Reed, 1960) from the Hemingfordian of Wyoming and the youngest of the Proscalopinae. The upper molars of *D. mimicus* are similar to the molars

of *Mesoscalops* figured by Reed in that both are large, have quadrate shape, little pinching of the labial cusps, and the size relationships and placement of the cusps are similar. *Domninoides mimicus* differs in having (1) anterior and posterior cingula extending from the lingual cusps to the labial side, and (2) enamel that does not extend below the gum line.

The massive, sturdy mandibles of *Domninoides mimicus* resemble those of *Scalopus* as do the L-shaped mandibular condyles. Unlike *Scalopus*, *Scapanus*, or *Parascalops* the angular process of *D. mimicus* is wider and more heavily built.

DESCRIPTION AND COMPARISON OF POSTCRANIAL BONES

Reed (1951) compared three soricoid insectivores (*Sorex*, *Neurotrichus*, and *Scapanus*) and discussed their increasing fossorial ability and subsequent changes in their limbs. Hutchison (1968), using Reed (1951) and Campbell (1939) as a base, explained and illustrated the increasing fossorial ability of all Recent moles and correlated this information with fossil moles from Oregon. With these papers in mind, I describe the postcranial elements of *D. mimicus* and, at the same time, compare them with the more fossorial Recent talpids, particularly *Parascalops*, *Scapanus*, *Scalopus*, and *Talpa*. Comparisons are also made with the few bones associated with other fossils.

The preserved proximal end of the left scapula is a sturdy, columnar fragment, broken slightly beyond the point where the supraspinatus fossa begins to flare out and where the subscapular surface and teres fossa are beginning to become more concave surfaces (fig. 5). The infraspinatus fossa is present as a deep groove that extends the length of the shaft to the acromion process. This fossa disappears in some of the more fossorial moles, the Talpini (*Talpa*) and the Scalopina (*Scapanus* and *Scalopus*). The acromion process and the glenoid fossa are both present. A foramen for the suprascapular nerve pierces the acromion process, a feature not present in the Talpini or Urotrichini. Of the Recent moles, *Parascalops* has both the infraspinatus fossa present for the whole length of the shaft and the foramen in the acromion process. When the elliptical
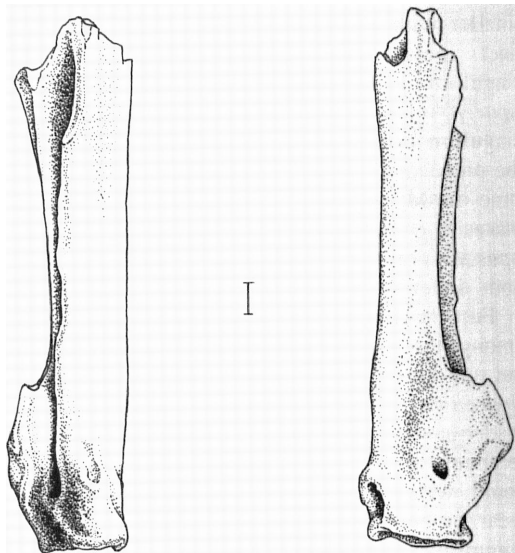

FIG. 5. Scapular fragment of *D. mimicus* (F:AM 74966) with dorsal view (on left) and ventral view (on right).

glenoid fossa is seen from an anterior view, *Domninoides mimicus* most resembles *Parascalops* but is larger. The scapula shaft fragment is thicker than that of any of the Recent moles. The two scapula fragments associated with the holotype of *D. mimicus* are also proximal ends and have the same features as F:AM 74966 though both are slightly smaller.

With the appearance of being short-shafted, the ulna is a thick robust bone from which the proximal crest flares out from the shaft at sharp angles, and the enlarged abductor fossa extends over half the length of the shaft (fig. 6). The similunar notch, greater than a semicircle and similar to that of *Scalopus* (Hutchison, 1968, fig. 13F), is formed by a small coronoid process and an enlarged processus anconaeus. On the proximal crest, muscle scars for the triceps resemble those on the ulnae of *Scapanus* and *Parascalops*, but they are more compressed laterally and appear wider. The ovoid, pitlike abductor scar lies posterior and internal to the lateral lip of the humeral articular facet, as in the Scalopina, but the radial articular process does not overhang the abductor fossa as it does in *Parascalops*, *Scalopus*, and *Scapanus* (and certainly not to the great extent as in *Talpa*); however, this may be due to wear. The small

fragment of ulna that is associated with the holotype has a less worn radial articular process that does overhang the fossa more than the material in the American Museum. The brachialis scar is elongate. Distal to the shaft, which is thicker than that in the Recent moles, the styloid process is enlarged and looks like the long, cylindrical ones in *Parascalops*, *Scalopus*, and *Scapanus*. The cuneiform articulation is a long, cylindrical articular surface but lacks the posterior terminal process (broken off). On the whole, the fossil ulna is as large as that in two of the largest and most fossorial Recent North American moles, *Scalopus aquaticus machrinoides* and *S. a. machrinus*, and bears a surprising resemblance to the first. The medial olecranon crest of the ulna of the fossil is more reminiscent of *Scapanus* (figure of *S. townsendii* in fig. 13F of Hutchison, 1968) which is emerging but not prominent (and completely lacking in most *Scalopus*), as in *Scapanus*.

The radius is a columnar, robust bone with a well-developed capitular process and groove for the tendon *M. abductor pollicis longus* (fig. 7).
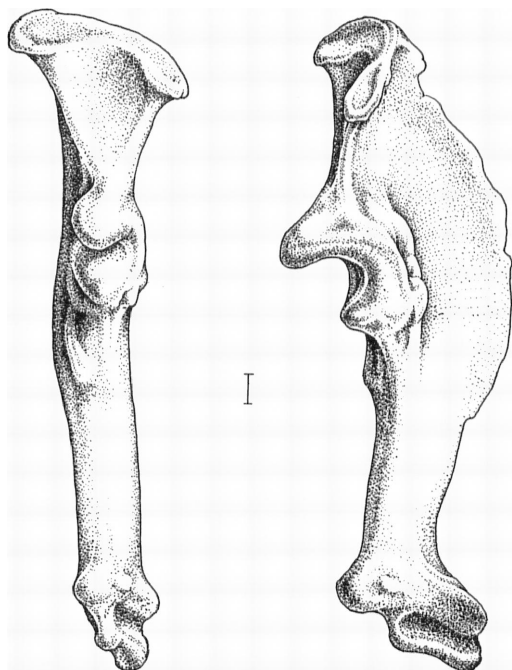

FIG. 6. Left ulna of *D. mimicus* (F:AM 74966) with anterior view (on left) and lateral view (on right).

As in *Parascalops*, the proximal border of the capitular process is level with the proximal border of the ulnar articulation. This proximal border is a rounded tuberosity in *Scalopus* and *Scapanus*. At the distal end the articular facets are developed for the lunar and scaphoid and give an outline that is scalloped, a feature typical of that in the more fossorial Recent moles. Generally, the fossil radius fragments of both F:AM 74966 and the type material of *D. mimicus* look like an enlarged, robust radius of *Parascalops*.

Domninoides mimicus has the well-developed femoral trochanters of the more fossorial species of moles (fig. 8). In general size *D. mimicus* corresponds with *Talpa* and the most fossorial living North American genera, *Scalopus* and *Scapanus*. The morphology of the proximal end closely resemble femora of *Scalopus* and *Parascalops*, especially in the relative sizes of the trochanters. These genera differ very slightly from *Scapanus* by less development of the greater trochanter and by having a more distinct third trochanter. Little difference exists in the distal end of femora of fossil and Recent fossorial moles.

The undescribed postcranial elements that are associated with the type of *D. valentinensis* Reed, 1962, which include radii, ulnae, and femora, are similar in morphology to the same bones of *Domninoides mimicus* but are smaller and slightly less massive in appearance. The semilunar notch of the associated ulnae is not so deep as in *D. mimicus* nor is the abductor fossa so wide (table 2).

Bones associated with *Scalopoides* have a delicate, slim appearance and are smaller than those of *Domninoides* (Hutchison, 1968, figs. 43, 44, and 45). The scapular fragment of *S. isodens* has a larger acromion process and deeper infraspinatus fossa; ulna with semilunar notch much less than a semicircle in shape, abductor fossa and proximal crest not so well-developed, relative shortness of olecranon process; radius lacking distinct groove for *M. pollicis longus* and oblique, not flat, proximal border of the capitular process, although the distal end is scalloped as in the Scalopini.

Postcranial comparisons between the proscalopine moles and *Scapanus* and *Scalopus* are taken up in Reed and Turnbull (1965). This endemic North American group has generally
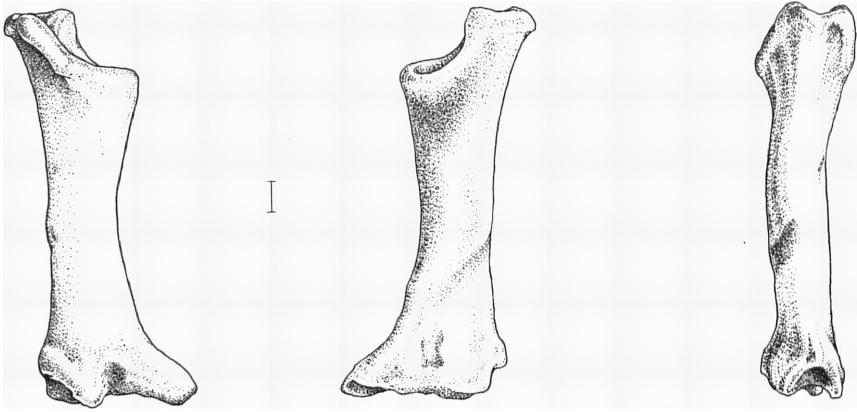
FIG. 7. Left radius of *D. mimicus* (F:AM 74966) with medial view on left, lateral view in middle, and posterior view on right.
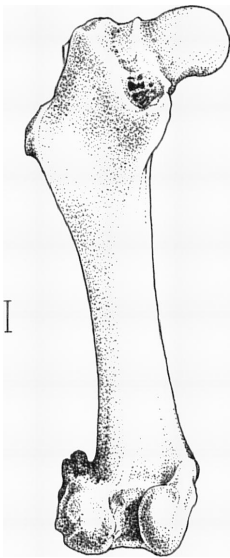

FIG. 8. Posterior view of femur of *D. mimicus* (F:AM 74966).

slimmer, less massive antebrachium than the Recent genera, and a humerus that is grossly different. Additional comparison with the more massive-boned *Domninoides* is not necessary.

DISCUSSION

Hutchison (1968) mentioned that loss of antemolars is associated with shortening of the rostrum, a frequent occurrence in mole history, and Zeigler (1971) wrote of the dental homologies of Talpidae and possible phylogenetic relationships based on the number and morphology of the antemolars. Both authors agree that loss of antemolars alone is not so valuable taxonomically but should be helpful when used with other criteria.

The incisor represented in the lower antemolars of *Domninoides mimicus* may well be I_1. I_2 is larger than I_1 in all three Recent genera (*Parascalops*, *Scapanus*, and *Scalopus*) and I_3 and the canine are variable in their appearance in *Scalopus* (Zeigler, 1971). The type of *D. valentinensis* appears to have a large alveolus for a hypertrophied I_2, a small alveolus for I_3 (rudimentary?), and a small peglike canine. The complete loss of I_3 and canine, because I_2 is enlarged is, therefore, not an unrealistic evolutionary change in the geologically younger *Domninoides mimicus*.

In Recent fossorial moles the first premolar of the lower jaw is either an unreplaced milk tooth as in *Parascalops* and *Scapanus* or not present at all, as in *Scalopus* (Zeigler, 1971). This tooth is missing in both *D. valentinensis* and *D. mimicus*. Also in *Scalopus* I_3 and the canine "prove to be extremely erratic in both their presence and degree of development" (Zeigler, 1971). This trend seems to have occurred in *Domninoides mimicus* as well.

In the upper dentition of living fossorial moles, all three incisors are present and I^1 is

the enlarged tooth (not in the Talpini). Specimens of *Scalopus* housed at the University of New Mexico have I^2 diminutive to I^3, which seems reasonable in order to make room for the enlarged I^1. *Domninoides mimicus* has an enlarged partial alveolus for I^1 (fig. 2) and a second incisor fragment. Whether this fragmented tooth is I^2 or I^3 is uncertain.

The lower molars of *Domninoides* resemble those of *Parascalops*, as Tedford (1961) mentioned, but are larger, bear less prominent metastylids, and have wider anterior cingula. *Domninoides* lacks the well-developed anterior cusp on the fourth lower premolar. Of the upper molars, those of *Domninoides* are more quadrate in shape (M^{1-2}), lack the paraconules on the lingual side (although a slight one is present on the unworn M^1 of the type material of *D. mimicus*), and bear cingula on the posterior face of M^1 and anterior and posterior faces of M^2. P^4 lacks the well-developed parastyle and a paraconule on the lingual side.

Tedford (1961) also compared the lower teeth of *Domninoides* with *Scapanus*. Major differences are that *Domninoides* molars are larger, bear cingula and metastylids; and that P_2

TABLE 2

Postcranial Measurements of *Domninoides mimicus* (F:AM 74966)
and *Domninoides valentinensis* (UCMP 36156, UCMP 36157)

Bone	Surface	Long axis	Measurement	F:AM 74966	UCMP 36156		UCMP 36157		
Scapula	Anterior	Long axis of glenoid fossa	Length	4.0	—	—	—		
			Width	2.6	—	—	—		
	Dorsal	Perpendicular to length of shaft	Width shaft posterior to acromion process	3.0	—	—	—		
Ulna[a]	Lateral	Aligned with columnar part of shaft using anterior edges of styloid process and proximal crest as orienting points	Greatest length	21.1	18.9	19.6	—		
			Shaft length, from center of semilunar to center distal articular surface	11.1	10.2	10.8	—		
			Olecranon length, from center semilunar to superior edge proximal crest[b]	8.8	7.6	7.6	—		
			Width abductor fossa, from posterior edge of fossa to coronoid process	5.2	4.2	—	—		
			Width shaft posterior to styloid process	2.5	1.9	2.0	—		
	Anterior	At right angles to long axis	Olecranon breadth	5.4	5.6	5.5	—		
Radius[c]	Lateral	Aligned with columnar part of shaft	Length	10.6	10.5	10.2	9.5	9.8	9.5
			Shaft length, from distal end to superior edge of capitular process	12.8	12.5	12.2	11.3	11.9	11.4
			Least width of shaft	2.2	1.9	2.0	2.0	1.8	1.8
			Width at distal end	5.2	—	4.9	4.4	—	4.4
Femur	Anterior	Aligned with columnar part of shaft	Greatest length	17.7	14.8	16.6	—		
			Least width of shaft	2.2	1.8	2.0	—		
			Width at distal end	5.1	4.2	4.7	—		
			Width across trochanters	5.5	4.3	5.6	—		

[a]See Hutchison, 1968, fig. 12.

[b]Many of these measurements follow Reed, 1956, though not exactly.

[c]See Hutchison, 1968, fig. 14.

is a double-rooted tooth. Upper molars of *Scapanus* are less quadrate in shape, have lingual shelves that end anterior to the metacone, and no cingula. Fourth upper premolar is bladelike and lacks the conical paracone and wide lingual shelf on *Domninoides. Scalopus* is similar to *Scapanus*, though more hypsodont, and need not be compared.

The dentition of *Domninoides mimicus* is striking in its large size and massive appearance. Development of the cingula on the upper and lower molars is conspicuous. Although certainly different in morphology, *Desmana* is a Recent genus with teeth similar in their massive, crushing appearance. The cingula development and the height of the crown in the teeth are probably inversely related modifications in talpids. What this has to do with fossorial ability of the mole, if anything, is unknown. In *Domninoides* the surface area of the molars for crushing food is certainly greater than that in the Recent fossorial moles. Cusps of the upper and lower molars (paracone and hypoconid) not only occlude with the hypoflexid and trigon basin, respectively, but also the metacones and protoconids occlude with the pitlike horizontal surfaces formed by the posterior and anterior cingula of the molars, which are spaced close together. The teeth of *Parascalops* are reminiscent of this arrangement but there are still open spaces between the molars (especially the uppers) and, because the molars have no large cingula against which opposing cusps can occlude, maintain a shearing appearance (i.e., vertical molar faces with little or no cingula). Molars of *Scapanus* and *Scalopus* being more hypsodont and having even less cingula (horizontal surfaces) than *Parascalops*, are all the more shearing and slicing in appearance.

Within the genus *Domninoides*, *D. mimicus* may well be the most fossorial form. It differs in number and morphology of lower antemolars from *D. valentinensis* and *D. riparensis*, as well as being larger than the latter. Postcranially, its bones are larger and there is greater development of the semilunar notch and abductor fossa on the ulna. *Domninoides valentinensis* from the Crookston Bridge Member of the Valentine Formation is a geologically older

animal than both the holotype of *D. mimicus* from the WaKeeney fauna of the Ogallala Formation in Kansas and F:AM 74966 from the Burge Member of the Valentine in Nebraska, and could easily be ancestral to the latter. *Domninoides riparensis* from the Wolf Creek Fauna of the undifferentiated Ogallala Group in South Dakota is not so specialized and whether or not it is an older animal geologically or simply less fossorial cannot be determined at this time.

In the proscalopine moles, which are fossorial and endemic to North America, the tendency has been for the molars to become square, the lingual shelf to broaden (Reed, 1961) and the cusps to become more hypsodont (Hutchison, 1972). A similar modification seems to occur between the less fossorial *Scalopoides* and the more specialized *Domninoides*. I agree with Hutchison (1968) that *Scalopoides*, which so far has appeared no earlier than the Hemingfordian (Wilson, 1960), may be ancestral to *Domninoides*. Postcranially, the delicate-boned *Scalopoides* has many features of the less fossorial Recent moles (Urotrichini). Phylogenetically, however, Hutchison (1968) groups *Domninoides* and *Scalopoides* together in the tribe Scalopini along with *Parascalops* and *Scapanulus*.

Any resemblance between the fossorial proscalopine moles and *Domninoides* is not a phylogenetic one but rather, one of convergence.

In a discussion of the functional significance of the postcranial elements, I should point out the general heavy, rugged appearance of the fossil bones, an appearance which is correlated with the increased stresses and leverages needed in the more fossorial moles. Additional, more specific features of adaptation to the subterranean life follow.

The infraspinatus fossa on the scapula disappears anteriorly in *Talpa*, *Scalopus*, and *Scapanus*, the more fossorial Recent moles. This fossa is present the length of the thick shaft fragment in *D. mimicus* and may mean that it is not as fossorial. The reduction process of the infraspinatus fossa involves the fusion of the axillary border and spine, which gives a cavelike appearance, and the disappearance of the fossa anteriorly. In this way more room is

made for the supraspinatus fossa and terres fossa and the respective muscles originating on those surfaces. Unfortunately, the vertebral end of the fossil scapula is not present and the reduction process cannot be verified as having started.

Although the humerus, which reflects much of the fossorial plasticity in talpids, is not present in the *D. mimicus* remains, the antebrachium, which is present, is just as adaptable and possibly more so than the humerus as the mole becomes more specialized for digging (Hutchison, 1968).

The short, massive appearance of the radius and ulna is characteristic of a talpid which has sacrificed speed above ground for strength below. Muscle scars on the wide proximal crest indicate a large area on which the M. triceps inserts, and similarly, a large abductor fossa for the M. abductor. The length of the olecranon process is nearly half the greatest length of the ulna (table 2) which makes for a long power arm, and the short shaft (relatively) makes for a short lever arm. Because the processus anconaeus (proximal lip) of the semilunar notch is greatly enlarged it will articulate with a deep olecranon fossa of the humerus; a fossa, which, in the more fossorial forms becomes progressively deeper and less prone to dislocation under the heavy digging stress. An additional strengthening of the elbow joint is the articulation between the large capitular process of the radius and the capitulum of the humerus. The distal end of the radius is not only wide but also scalloped in appearance. Both are features which allow greater articulation with the manus for the fore and aft motion of digging and are typical of the more fossorial Recent moles.

Few major changes occur in femora of soricoids except that the more fossorial moles have better developed processes on the proximal end of the bone (Reed, 1951). The Clarendonian mole has a femur with well-developed processes.

In many ways *Domninoides mimicus* is reminiscent of *Scalopus* which Campbell (1939) believed to be the most fossorial North American mole. Its rostrum is short and has lost a premolar, a canine, and an incisor; the shape of the mandible and dentary condyles are similar. In-consistencies exist, however, because the scapula and proximal end of the radius resemble the same bones in *Parascalops*, a more generalized talpid (Campbell, 1939). There is also some similarity in the molars of *Parascalops* and *Domninoides*. The resemblance between the fossil and Recent *Scalopus* is, again, not a phylogenetic one but one of ecological convergence. Both *Scalopus*, especially the largest subspecies from the midwest (Jackson, 1915), and *Domninoides* from the Clarendonian of north-central Nebraska are from a plains environment and are highly fossorial creatures.

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